To what degree do preferred prey abundance and temperature influence growth rates of larval yellow perch in Lake Erie?

Undergraduate Honors Research Thesis

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Abstract

Growth during the larval stage can have important effects on future foraging and growth performance, as well as subsequent survival and recruitment to the fishable population. Preferred prey abundance and temperature have both been shown to influence larval fish growth in a variety of ecosystems. Toward improving our understanding of how these factors influence larval yellow perch (*Perca flavescens*) growth in Lake Erie, I examined the relationship between temperature, ambient zooplankton abundance, and larval yellow perch diets and growth rates in Sandusky Bay (Ohio) during 1994–1998, 2017, and 2018. I hypothesized that both preferred prey abundance and temperature would enhance the growth of larvae. Using linear modeling, I found that preferred zooplankton prey availability was unrelated to larval yellow perch growth (cyclopoid: $t = 3.90$, $p = 0.06$; calanoid: $t = 1.06$, $p = 0.40$), which was unexpected. Similarly, temperature during the time when larval yellow perch were caught was unrelated to growth ($t = -3.80$, $p = 0.06$). Furthermore, while mean April temperature (an indicator of the spring thermal conditions) was related to larval yellow perch growth rate, this relationship was unexpectedly negative ($t = -5.14$, $p = 0.04$). Because I am uncertain of why my expectations were not borne out, I recommend future research to evaluate other metrics of spring and prior winter conditions (*e.g.,* overwinter ice-cover, winter degree days for adult yellow perch, spring onset, spring degree days) to identify the mechanisms influencing larval yellow perch growth.

Introduction

Growth can influence the recruitment of fish by determining how long individuals remain vulnerable to predation and starvation during early life stages (Miller *et al.* 1988, Post and Evans 1989, Houde 2008), yet, our understanding of the factors that regulate early-life growth in most ecosystems is limited. A range of factors, both biotic and abiotic, can influence growth. For example, inadequate prey availability can slow growth and lead to starvation (Bremigan *et al.* 2003, Graeb *et al.* 2004, Fulford *et al.* 2006a). Likewise, temperature can influence growth directly by altering metabolic processes (Ney and Smith 1975, Power and Heuvel 1999, Ludsin *et al.* 2014) and indirectly by influencing prey availability and maternal effects, among other things (Durant *et al.* 2007, Kristiansen *et al.* 2011, Farmer *et al.* 2015). Because the relative importance of these factors typically varies throughout ontogeny, among ecosystems, and through space and time, critical knowledge gaps exist regarding their relative influence on foraging, growth, and eventual recruitment (Claramunt and Wahl 2000, Ludsin *et al.* 2014). Understanding the drivers of early life performance in fish is especially critical given the increasing degree of anthropogenic change that many ecosystems are experiencing (Prout *et al.* 1990, Nicholls and Hopkins 1993, Durant *et al*. 2007).

One ecosystem that has been experiencing a great deal of environmental change is Lake Erie (USA–Canada). Both temperature and zooplankton abundance have increased due, in part, to climate change (Hayhoe *et al.* 2010, Farmer *et al.* 2015). Invasive species introductions and variation in nutrient inputs have further altered zooplankton abundance in Lake Erie (Nicholls and Hopkins 1993, Briland 2018). Our understanding of the effects of these changes on fish recruitment has been improving but remains incomplete (Ludsin *et al.* 2014). It is important that we continue to improve this understanding, as doing so may help us to understand the

demographics and dynamics of fish populations and the vital fisheries that they support (Houde 2008, Ludsin *et al.* 2014, Pritt *et al.* 2014).

One population for which we lack a full understanding of the recruitment process is western Lake Erie yellow perch (*Perca flavescens*), which has been highly variable during recent decades in Lake Erie (Belore 2020). This population is of both ecological and economic importance, and helps support the lake's largest commercial fishery and second-largest recreational fishery (Kayle 2018). While much research has been conducted on Lake Erie yellow perch, gaps remain in our understanding of the factors that affect growth of larvae, which appears important to future survival (Reichert *et al.* 2010, Ludsin *et al.* 2014). For example, laboratory experiments have shown that the abundance of preferred prey items, which may be particularly important to larval yellow perch, can have substantial effects on larval yellow perch growth (Confer and Lake 1987, Graeb *et al.* 2004, Fulford *et al.* 2006a). However, less is known about how prey availability affects the growth of yellow perch larvae in Lake Erie (Reichert *et al.* 2010, Marin Jarrin *et al.* 2015, Marin Jarrin *et al.* 2017). Additionally, while temperature has frequently been shown to have a direct, positive effect on larval fish growth (Ludsin 2000), investigations of its effects on larval yellow perch growth have yielded mixed results (Henderson 1985, Post and McQueen 1994, Power and Heuvel 1999). Consequently, our understanding of the relative importance of preferred prey abundance and temperature on yellow perch growth in Lake Erie remains speculative.

Toward filling these gaps, I estimated the average annual growth rates of yellow perch larvae collected from Sandusky Bay, Lake Erie, during seven years (1994–1998, 2017, and 2018). I then identified preferred prey taxa, estimated the abundance of these taxa in the environment, and explored how variation in their abundance, as well as temperature, related to

larval yellow perch growth rate. Given the results of previous research in other ecosystems (Mills *et al.* 1989, Power and Heuvel 1999, Bremigan *et al.* 2003), I hypothesized that preferred prey abundance and temperature would both positively influence Lake Erie larval yellow perch growth rate. I predicted that preferred prey abundance would have a stronger effect on growth than temperature because of the inconclusive findings of previous studies that explored the effects of temperature on larval yellow perch growth (Henderson 1985, Post and McQueen 1994). By testing this hypothesis, I sought to improve our understanding of the factors that affect larval yellow perch growth, which could potentially help us understand the causes of annual variation in their recruitment in Lake Erie.

Methods

Study species

Early-life conditions, especially temperature and prey availability, are important to larval yellow perch growth, survival, and subsequent recruitment to older life stages (Dettmers *et al.* 2003, Ludsin *et al.* 2014). Yellow perch larvae hatch at 4–7 mm in total length (TL) during late April through early June in western Lake Erie (Mansueti 1964, Auer 1982, Brown *et al.* 1996, Ludsin 2000), and feed solely on zooplankton in the water column beginning a few days after hatching (Brown *et al.* 1996, Reichert *et al.* 2010, Marin Jarrin *et al.* 2015). The gape width of larvae limits the size of zooplankton that individuals can consume (Schael *et al.* 1991, Bremigan *et al.* 2003) and their poor swimming capabilities (Houde 1969) may restrict the ability of larvae to catch fast or evasive prey taxa (*e.g.,* large, calorific calanoid copepods; Nassal *et al.* 1998). Therefore, unavailability of certain prey may negatively affect larval yellow perch growth, which

could reduce survival to older life stages (Miller *et al.* 1988). For this reason, I used somatic growth rate as a proxy for eventual recruitment.

Field collections

During 1994–1998, 2017, and 2018, larval yellow perch were collected weekly during late April through June (Table 1) from multiple locations (n = 3–6) in Sandusky Bay, Lake Erie, using paired 0.5-m diameter bongo nets (2017–2018), 1-m diameter ichthyoplankton nets (2017–2018), or 1 m × 2 m neuston nets (all years). All nets were towed for 5 to 10 min at the surface. Nets were equipped with 500-µm mesh early in the sampling season, with mesh size increasing to 1000 µm later in the season to allow for faster tow speeds necessary to capture larger, faster larvae. Captured larvae were preserved and stored in 95% ethanol until laboratory analysis, where yellow perch were identified under dissecting microscopes using myomere counts that differentiated between species of similar appearance (Auer 1982).

Zooplankton were collected at each site from which larval yellow perch were collected using 0.3-m diameter nets during 1994–1998 and 0.5-m diameter nets during 2017–2018. Nets were equipped with 64-µm or 153-µm mesh during 1994–1998, whereas only 64-µm mesh nets were used during 2017–2018. The volume of water sampled by nets was calculated as the product of the depth of each vertical tow and the area of the net mouth. These volumes were then corrected for the filtration efficiency of the mesh under turbid conditions (35.4% efficiency for 64-µm mesh, 100% efficiency for 153-µm mesh; Mack *et al.* 2012). Zooplankton were preserved in 70% ethanol during 1994–1998 and 40% sugar formalin during 2017–2018 until samples were processed in the laboratory.

Zooplankton quantification methods varied slightly between the two time periods. During 1994–1998, subsamples of zooplankton were counted until at least 50 individuals of the same

taxonomic group (typically genus) were identified from each sample, whereas during 2017–2018, counts were conducted until at least 100 individuals of the same taxonomic group (typically genus) were identified in each sample. Smaller taxa (*i.e.,* copepod nauplii, rotifers, and dreissenid veligers) were identified but excluded from analyses because they were too small to be sampled reliably by the 153-µm nets used during 1994–1998. These species also were rare in diets (<4% by abundance and <1% by biomass). While previous research has shown that the two counting methods used to estimate zooplankton abundance differ in their precision, my exclusion of rare and small taxa and use of broad taxonomic groupings likely improved their comparability (Mack *et al.* 2012). The length (nearest 0.01 mm) of the first 22 individuals identified from each taxon was measured during 1994–1998, whereas only the first 20 individuals were measured during 2017–2018. Zooplankton biomass (µg/L, dry mass) was estimated using length-mass equations (Dumont *et al.* 1975, Culver *et al.* 1985).

Prey availability and diet selectivity

The contents of larval yellow perch guts (undifferentiated stomach and intestinal tract) were analyzed until at least 10 individuals with non-empty guts were processed from each site and date. The diets of all yellow perch larvae were examined from each site and date where fewer than 10 individuals were collected. The TL of all larvae processed for diet analysis were measured to the nearest 0.1 mm with individuals measuring over 22.7 mm in TL (the maximum TL of larvae collected during 2017) being excluded from all analyses to ensure that the developmental stages and, therefore, feeding habits of larvae included in analyses remained consistent across years. Dry masses of larvae (nearest 0.1 mg) were calculated using a length-mass regression developed using yellow perch larvae 9.5–22.5 mm in TL collected from the

western basin of Lake Erie during 1995 (E. Roseman, USGS, and S. Ludsin, The Ohio State University, unpublished data).

Zooplankton consumed by larval yellow perch were identified to the same taxonomic resolution as zooplankton in the field. Similar to ambient zooplankton, the lengths (nearest 0.01 mm) of the first 20–22 individuals of each prey taxon encountered in guts were measured. Diet item biomass was estimated using the same length-mass equations as for ambient zooplankton biomass (Dumont *et al.* 1975, Culver *et al.* 1985) and the total diet biomass of each larva was calculated as the summed biomass of each identifiable diet item (*i.e.*, unidentifiable diet items were not included in the calculation).

Larval yellow perch selection for each prey taxon was calculated using Chesson's α (1978). Chesson's α compares the relative frequencies of prey types in the larval diet to those in the environment:

$$\alpha_i = \frac{r_i / n_i}{\sum_{i=1}^{m} r_i / n_i}$$

where *r* and *n* are the relative abundance of prey item *i* in the larval gut and in the environment, respectively, and *m* is the number of prey taxonomic groups. Chesson's α was calculated for seven diet item categories (*i.e.*, *Bosmina*, calanoids, *Chydorus*, cyclopoids, *Daphnia*, *Diaphanosoma*, and *Leptodora*) across all yellow perch larvae collected in a year. These seven taxa comprised >94% of biomass consumed and were also reliably sampled from the environment by both the 64-µm and 153-µm mesh nets (Mack *et al.* 2012). For my analyses, selection for a prey category was deemed positive or negative in a 3-mm larval yellow perch TL bin if the interquartile range (IQR) of Chesson's α values for that prey type across all larvae with TLs in that bin did not encompass the Chesson's α value of 1/7. This value indicates neutral selection (*i.e.*, the proportion of that taxa in the diet matches the proportion of that taxa in the

environment) and was calculated as 1/n, where n is the number of prey taxa (*i.e.*, 7; Chesson 1978).

Mean ambient density (individuals/L) was calculated during each year for the zooplankton taxa that were consistently positively selected (*i.e.*, preferred) in every year. To calculate this annual mean, mean densities across sites within each week were calculated, with densities across all weeks in which larvae were collected averaged afterwards. The same was done for ambient zooplankton biomass (µg/L, dry mass).

To account for the possibility that availability of preferred zooplankton prey taxa is only important for larval growth when those taxa are preferred during larval ontogeny, the ambient density and biomass of preferred prey taxa were also calculated during only the time period when each was preferred. Our methods for delineating periods of preference for each prey taxon and calculating abundance during the corresponding periods of preference are described in Appendix A (Supplemental Fig. A1). They will not be discussed here further because preferred prey availability during these periods was less closely related to yellow perch growth than preferred prey availability during the entire sampling period (Supplemental Tables A1 and A2) and was thus excluded from further analyses.

Calculating growth

Average daily growth rates (mm/d) of larvae were estimated as $(TL_1 - TL_0)/t$, where TL_1 is the average length of larvae collected during a week, TL_0 is the average length of larvae collected during the prior week of sampling, and t is the number of days between the midpoint of each sampling event. The average daily growth rates of larvae between each week of sampling were averaged during each year to create an index of daily growth rates.

Temperature

I calculated two temperature metrics, given that temperature can affect the phenology of yellow perch spawning (and hence, larval appearance in the water column), as well as growth through metabolic processes (Kayes and Calbert 1979, Kaemingk *et al.* 2014). One temperature metric accounted for interannual differences in spring conditions and the appearance of larval fish in the water column (mean April temperature), whereas the second accounted for direct influences of temperature on larval yellow perch growth rates (termed "mean growing temperature"). Complete water temperature datasets were unavailable for each year. However, because air temperature is closely correlated with water temperature and is therefore an appropriate substitute for water temperature (McCombie 1959, Livingstone and Lotter 1998), I used air temperature data from the National Oceanic and Atmospheric Administration's National Climatic Data Center (https://www.ncdc.noaa.gov/) to calculate mean April temperature and "mean growing temperature" (*i.e.*, average temperature during only the period that larvae were collected) during 1994–1998, 2017, and 2018 (Supplemental Table A1). Each annual temperature metric was calculated by averaging the mean daily temperatures across the specified period during each year, where mean daily temperature was calculated as the average of the high and low temperature on that day.

Data analysis

I used a general linear model to determine the extent to which variation in prey availability, mean April temperature, and mean growing temperature explained variation in the annual growth rates of yellow perch larvae. Prior to their inclusion in the model, I calculated Pearson's correlation coefficients for all pairs of variables, including response (growth rate) and all predictor variables. Predictor variables that were closely correlated with other predictor variables (|Pearson's r| > 0.7) were excluded from further analyses, including measures of

ambient copepod biomass (resulting in my use of ambient copepod density in my general linear model). Residuals were normally distributed, as assessed with a Q-Q plot, indicating that my data met assumptions of normality for a general linear model. All calculations and analyses excluded larvae from weeks in which fewer than 10 yellow perch larvae (with identifiable diet items in the gut, for diet analyses) were collected.

Results

Environmental conditions

Environmental conditions varied within and among years. Total ambient zooplankton density varied through time, with no consistent pattern in the relative abundance of different taxa within years or among them (Fig. 1). While copepod density also was highly variable within and among years, general trends of decreasing cyclopoid density and increasing calanoid density during May through June were evident during most years (Fig. 2). Mean April temperature ranged from 6.2ºC to 12.1ºC, and mean growing temperature ranged from 14.5ºC to 19.4ºC (Table 1). Ambient zooplankton density metrics were poorly correlated with temperature metrics (|Pearson's r| < 0.7; Supplemental Tables A1 and A2).

Diet biomass

Yellow perch diets and lengths varied predictably through time. The total biomass of identifiable diet items was positively related to the TL of yellow perch larvae throughout each year (Fig. 3). Total mass-specific consumption was more variable, but also generally increased during each year (Fig. 3C). Gape size appeared to limit the prey sizes that larvae consumed, as the size of the largest prey items consumed increased with gape size (Fig. 4).

Yellow perch diet composition did not reflect the relative abundance of zooplankton taxa in the environment. While the relative abundance of zooplankton taxa varied within and among

years (see Fig. 1), the most abundant taxon in diets was either cyclopoids or calanoids on all dates sampled during all years (Fig. 5). During most years, the number of cyclopoids consumed by larvae decreased through time, while the number of calanoids consumed increased through time (Fig. 6A, 6B). When I standardized copepod consumption by yellow perch dry mass, I found that cyclopoid consumption did generally decline throughout the sampling period (Fig. 6C). However, trends of increasing calanoid consumption appeared to be confounded by increases in yellow perch mass through time (Fig. 6D). Trends in copepod consumption appeared to align with the general decrease in ambient cyclopoid density and general increase in ambient calanoid density observed within years (Fig. 2).

Prey selectivity

Even so, my prey selectivity calculations indicated that copepod consumption was not simply dictated by ambient zooplankton abundance. Chesson's α values indicated that larvae consumed disproportionately large numbers of cyclopoids at small larval TLs and calanoids at large larval TLs relative to their abundance in the environment (Fig. 7). During all years except 1996, this pattern of copepod preference was characterized by strong positive selection (Chesson's α IQR > 1/7) for cyclopoids at small larval TLs and neutral to negative selection for all other taxa. During 1996, selection for cyclopoids was neutral among small larvae (Chesson's α IQR encompassed 1/7). By contrast, large larvae exhibited strong positive selection (Chesson's α IQR > 1/7) for calanoids with neutral to negative selection for all other taxa during all years except for 2017 and 2018. During these latter two years, however, no more than 10 larvae with diet items in the gut belonging to any 3 mm TL bin > 14 mm were collected. In fact, except for cyclopoids and calanoids, selection was negative (Chesson's α IQR < 1/7) at all larval yellow perch lengths for every zooplankton taxon other than *Diaphanosoma*. Selection for

Diaphanosoma was neutral (Chesson's α IQR included 1/7) for 20–23 mm larvae during 1994 and 11–20 mm larvae during 1996. Given these collective findings, cyclopoid and calanoid abundance appeared more likely to influence larval yellow perch growth than other taxa.

Growth

Variation in annual average daily growth rates among years was low compared to that observed in similar studies of larval yellow perch growth (Weber et al. 2011, Kaemingk et al. 2014). Annual average daily growth rates of yellow perch larvae ranged from 0.23 mm/d during 1995 to 0.35 mm/d during 2018 (Fig. 8). However, variation in weekly average daily growth rates was high within years (Fig. 9). The weekly average daily growth rates of larvae increased during May through June during most years (Fig. 9).

To help explain annual growth variation, I built a general linear model that predicted annual larval yellow perch growth from mean April temperature, mean growing temperature, ambient cyclopoid density, and ambient calanoid density. This modeling showed that April temperature (my proxy for overall spring conditions) was the only significant predictor of growth and was negatively related to growth (Table 2 Fig. 10C). Larval yellow perch growth was marginally negatively related to mean growing temperature (Table 2, Fig. 10D). Ambient cyclopoid density was marginally positively related to growth (Table 2, Fig. 10A), while ambient calanoid density was unrelated to growth (Table 2, Fig. 10B).

Discussion

To improve our understanding of the factors that drive larval yellow perch growth in Lake Erie, I explored the effects of zooplankton prey abundance and thermal conditions on foraging and growth performance. Surprisingly, I did not observe a significant effect of growing temperature or preferred prey abundance on annual larval yellow perch growth rate. Instead, I

found that larval yellow perch growth rates were higher during years with cooler April temperatures than warmer ones. This finding suggests that increasing spring temperatures resulting from climate change (Hayhoe *et al*. 2010) could negatively affect larval yellow perch growth in temperate ecosystems such as Lake Erie. Below, I discuss these findings in more detail, including how they relate to understanding variation in yellow perch recruitment to older life stages.

Of the predictors included in my model, I was most surprised to find that preferred prey abundance was unrelated to larval yellow perch growth rate. Positive relationships between zooplankton prey density and larval yellow perch growth have been observed in both laboratory (Graeb *et al.* 2004, Fulford *et al.* 2006a) and field studies (Noble 1975, Mills and Forney 1981, Mills et al. 1989, Prout et al. 1990, Bremigan et al. 2003, Dettmers et al. 2003). The lack of relationship between preferred prey abundance and growth rates that I observed could conceivably result from a high abundance of zooplankton in Lake Erie, which could have functionally eliminated the dependency of larval yellow perch growth rate on variation in zooplankton abundance. Similar explanations have been proposed for the lack of relationships, and even negative relationships, between prey abundance and larval growth rates in other highly productive systems (Mooij *et al.* 1994, Kaemingk *et al.* 2014). However, I observed zooplankton densities in Sandusky Bay that were similar to those in Green Bay (Lake Michigan) during years when larval yellow perch growth rates were found to be related to prey abundance (Bremigan *et al.* 2003). Additionally, prey densities in Sandusky Bay were similar to those at which prey densities were shown to influence larval yellow perch growth rates in laboratory experiments (Fulford *et al.* 2006a). Therefore, it is unclear why I observed no relationship between prey density and yellow perch growth in Sandusky Bay.

I was also surprised to find that annual average growing temperature was not positively related to annual larval yellow perch growth rate. Positive relationships between spring temperatures in the ranges that I observed and larval yellow perch growth have been documented in several ecosystems (Power and Heuvel 1999, Weber *et al.* 2011, Kaemingk *et al.* 2014). Similar relationships between temperature and growth have also been documented in countless other species (Dwyer and Piper 1987, Mooij *et al.* 1994, Claramunt and Wahl 2000, Del Toro-Silva *et al.* 2008). However, it is not uncommon for larval yellow perch growth to be unrelated to water temperature. For example, larval yellow perch growth was unrelated to spring temperatures in Lake Huron (Henderson 1985) and in several Ontario lakes (Post and McQueen 1994). This lack of consistency in the relationship between temperature and larval yellow perch growth among ecosystems suggests that other environmental attributes more strongly influence larval yellow perch growth than ambient temperature. Perhaps other factors associated with winter temperatures or April temperatures more heavily influence larval yellow perch growth rates in Sandusky Bay, masking the effects of growing temperature on larval growth rates.

Additionally, April temperature may be an indicator of annual variation in an aspect of the early-life environment that I did not include in my model. A variety of factors, such as predation, maternal effects, or competition, could have been correlated with April temperature. These factors could have overwhelmed the influence of both prey abundance and growing temperature on yellow perch growth and resulted in a spurious correlation between April temperature and yellow perch growth. One such factor that I did not consider in my model is predation. Predators tend to feed selectively on larval fish, especially small individuals, with size-specific predation patterns often varying among species and through time (Post and Prankevicius 1987, Miller *et al.* 1988, Rice *et al.* 1993a, Fulford *et al.* 2006b). Additionally,

effects of winter temperatures on fish populations are likely to vary among species (Shuter and Post 1990). Therefore, if April temperature is related to overwintering temperature, then I could expect to see variation in the relative abundance of predator species and size variation during spring, leading to variation in size-specific predation among years. However, to predict the relationship between April temperature and predation-driven variation in larval yellow perch growth rates, I would need to learn which fish species prey most heavily on yellow perch larvae in Sandusky Bay, which sizes of larvae are preyed upon most heavily, and how these predator populations are influenced by winter temperature. It would be worthwhile to explore this in the future.

Maternal effects associated with winter temperatures could also contribute to the negative relationship that I observed between April temperature and larval yellow perch growth rates. Winter duration and yellow perch egg size and quality during the following spring appear to be positively correlated in Lake Erie, translating into increased larval size at hatch and greater egg energetic content following long winters than following short winters (Farmer *et al.* 2015). Both of these advantages could enable yellow perch larvae to take advantage of a greater variety of prey soon after hatching, translating to faster growth (Hjort 1914, Schael *et al.* 1991, Farmer *et al.* 2015). If years with longer winters have cooler springs (Aprils), perhaps the negative relationship that I observed between April temperature and growth results from maternal influences.

Competition among larvae is a third factor that was not considered in my model which could have influenced growth rates. Larval yellow perch growth rates have been shown to be negatively related to larval fish density in many ecosystems (Henderson 1985, Post and McQueen 1994, Post *et al.* 1997, Irwin *et al.* 2009). Density-dependent larval growth could

result from competition for prey resources (Post and McQueen 1994). However, if competition for prey was occurring, I would expect to see reductions in preferred prey abundance during years when competition among larvae for prey caused reduced growth rate (Welker *et al.* 1994, Roseman *et al.* 1996). I did not observe a significant relationship between preferred prey density and larval yellow perch growth rates among years. Thus, competition among larvae for zooplankton prey likely did not contribute substantially to the lack of relationship I observed between yellow perch growth and both prey abundance and growing temperature.

Finally, the growth rate estimates that I calculated using weekly changes in average larval yellow perch TL may have been biased by variability in the timing of hatching and (or) growth-dependent ontogenetic habitat shifts. Because yellow perch larvae in Sandusky Bay have a protracted spawning season (Ludsin 2000), young, small larvae may have entered the population after the first sampling date, causing growth to be underestimated. Similarly, it is possible that some individuals exited the sampled population before the end of the sampling season, becoming demersal or attaining swimming capabilities that enabled them to evade capture in surface-towed nets. The removal of these large individuals from the sampled population during the sampling season could have caused me to underestimate larval yellow perch growth. Additionally, selective predation upon either small or large larvae could remove individuals of certain sizes from the sampled population during the sampling season, biasing growth estimates (Rice *et al.* 1993b).

While my larval yellow perch growth estimates may have been biased by some combination of these aforementioned factors, they were similar to the average growth rates calculated for pelagic yellow perch larvae in two other ecosystems for which I found comparable data: Pelican Lake, Nebraska (Kaemingk *et al.* 2014) and Lake Michigan (Weber *et al.* 2011). In

Pelican Lake, growth rates estimated using changes in average larval yellow perch TL ranged from 0.09 to 0.50 mm/d during the early larval period and 0.09 to 0.39 mm/d during the late larval period (Kaemingk *et al.* 2014). In Lake Michigan, growth rates calculated using back-calculated length estimates from otolith circuli ranged from 0.11 to 0.19 mm/d during the early larval period and 0.36 to 0.52 mm/d during the late larval period (Weber *et al.* 2011). Growth rate estimates from otolith circuli are unlikely to be biased by the same factors as growth rates estimated using differences in total length across weeks and may be more accurate for this reason (Francis and Campana 2004). Unfortunately, it was not feasible to estimate larval yellow perch growth from otoliths for my study, but doing so could be considered in any follow-up study.

In conclusion, environmental conditions during the larval stage appear important to yellow perch feeding and growth. However, neither prey availability nor temperature accounted for growth variation in the ways that I expected. The unexpected negative relationship between April temperature and larval yellow perch growth highlights the need for more work to understand the causal mechanisms. By better understanding this relationship, our ability to understand recruitment may increase, given the seeming dependence of recruitment of Great Lakes fishes like yellow perch on physical processes during early life (Ludsin *et al.* 2014). Continued research exploring how early-life conditions affect larval fish growth in Lake Erie and elsewhere could help to characterize the conditions under which system-specific responses may arise and offer insight into some of the less commonly recognized factors that regulate larval fish growth in other ecosystems. Such understanding should ultimately help researchers understand and predict growth variation in fish populations and, in turn, subsequent recruitment to older life stages.

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Table 1. Range of sampling dates for yellow perch larvae, mean (± 1 standard error, SE) April temperature (ºC), mean (± 1 SE) growing temperature (ºC), and number of larvae collected in Sandusky Bay, Lake Erie, and analyzed for gut content analysis during 1994–1998, 2017, and 2018.

Year	First sampling date	Last sampling date	April temperature	Growing temperature	Number of larvae collected	Number of diets analyzed
1994	5/3	6/22	10.4 ± 1.1	17.3 ± 0.8	1901	374
1995	5/2	6/21	8.2 ± 0.8	18.2 ± 0.6	695	198
1996	5/13	6/25	7.8 ± 1.0	19.3 ± 0.8	345	123
1997	5/13	6/23	7.9 ± 0.9	15.6 ± 0.7	1116	121
1998	5/6	6/9	10.0 ± 0.6	19.2 ± 0.5	1128	231
2017	4/26	5/31	12.1 ± 0.8	14.5 ± 0.7	938	178
2018	5/8	5/30	6.2 ± 0.9	19.4 ± 0.9	478	67

Table 2. Results from the general linear model examining the relationship between ambient cyclopoid density, ambient calanoid density, mean April temperature, and mean growing temperature and annual average daily growth rate of larval yellow perch in Sandusky Bay, Lake Erie, during spring 1994–1998, 2017, and 2018. Significance tests were evaluated with an $\alpha = 0.05$. Bolded values indicate p-values < 0.05.

Predictor	$\mathbf{t_{df1,df2}}$	**p**
Cyclopoid density	$3.90_{1,2}$	0.06
Calanoid density	$1.06_{1,2}$	0.40
April temperature	$-5.14_{1,2}$	**0.04**
Growing temperature	$-3.80_{1,2}$	0.06

List of figures

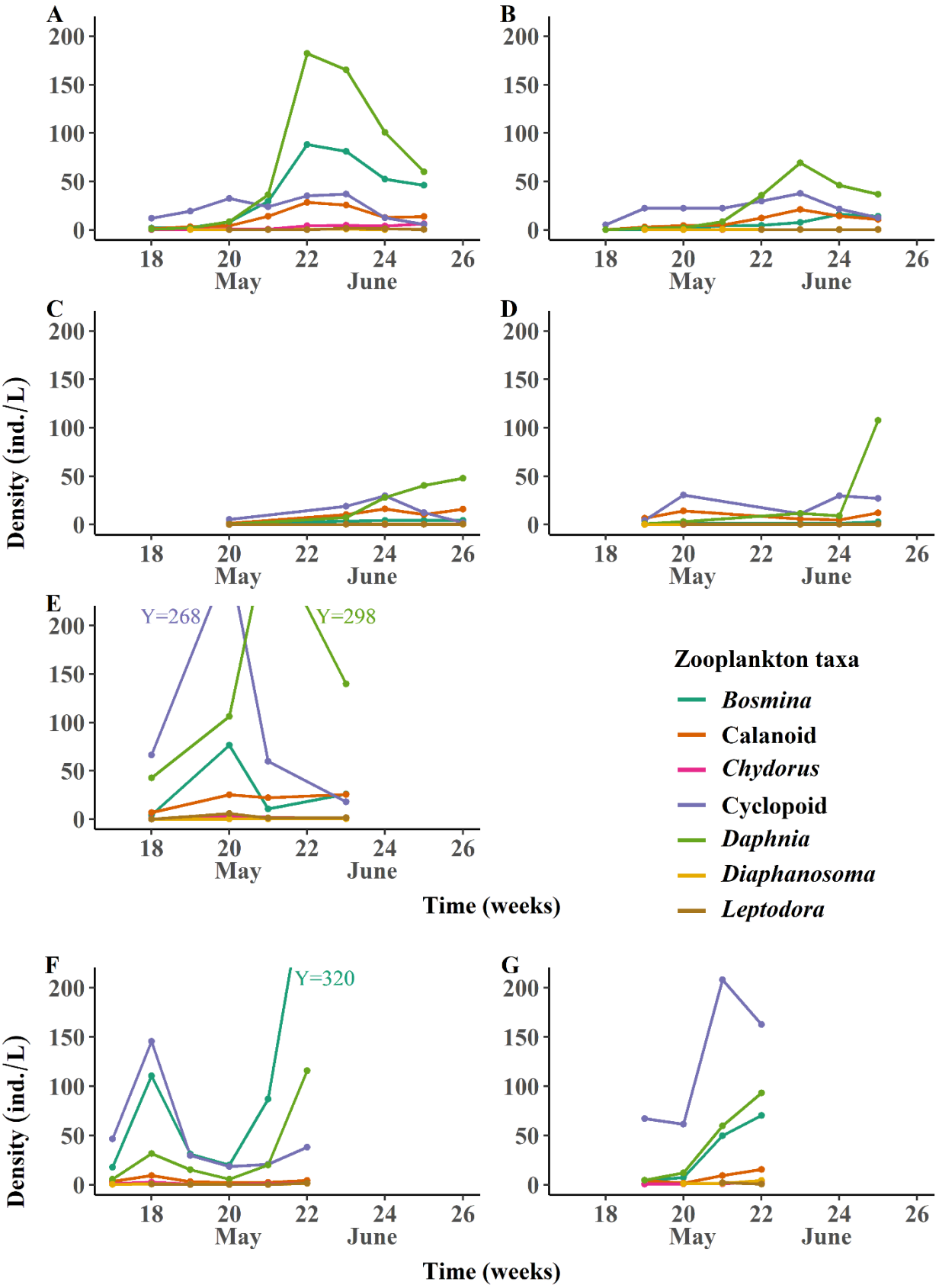

A
B
C
D
E
F
G
Density (ind./L)
Time (weeks)
May
June
Y=268
Y=298
Y=320
Zooplankton taxa
Bosmina
Calanoid
Chydorus
Cyclopoid
Daphnia
Diaphanosoma
Leptodora

Figure 1

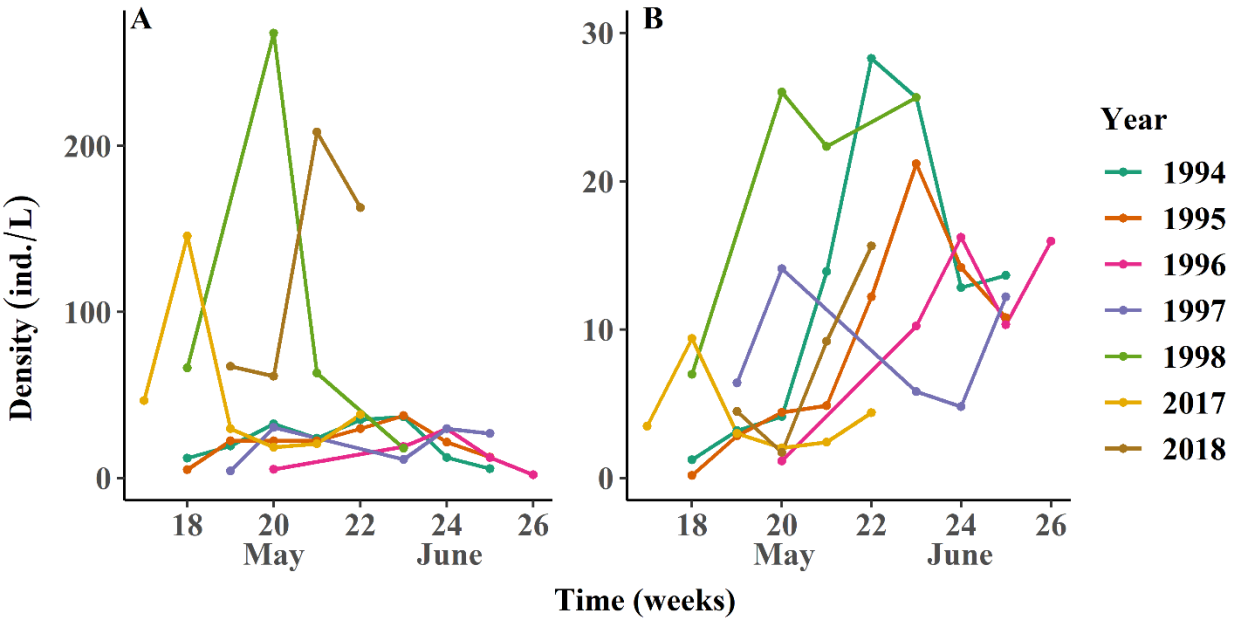

A
B
Density (ind./L)
200
100
0
30
20
10
0
18
20
22
24
26
May
June
Time (weeks)
Year
1994
1995
1996
1997
1998
2017
2018

Figure 2

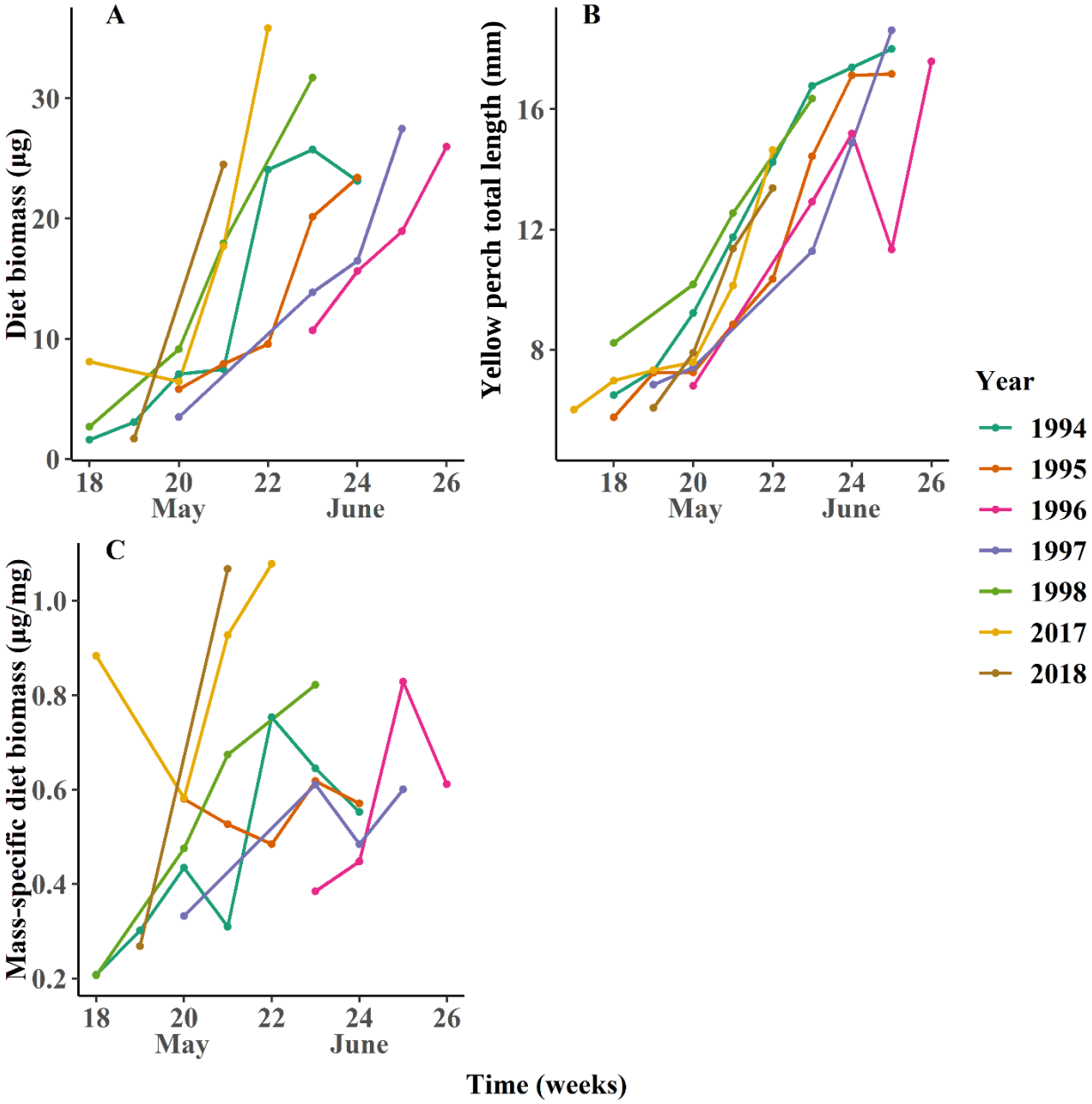

A
B
C
Diet biomass (µg)
Yellow perch total length (mm)
Mass-specific diet biomass (µg/mg)
0
10
20
30
8
12
16
0.2
0.4
0.6
0.8
1.0
18
20
22
24
26
May
June
Time (weeks)
Year
1994
1995
1996
1997
1998
2017
2018

Figure 3

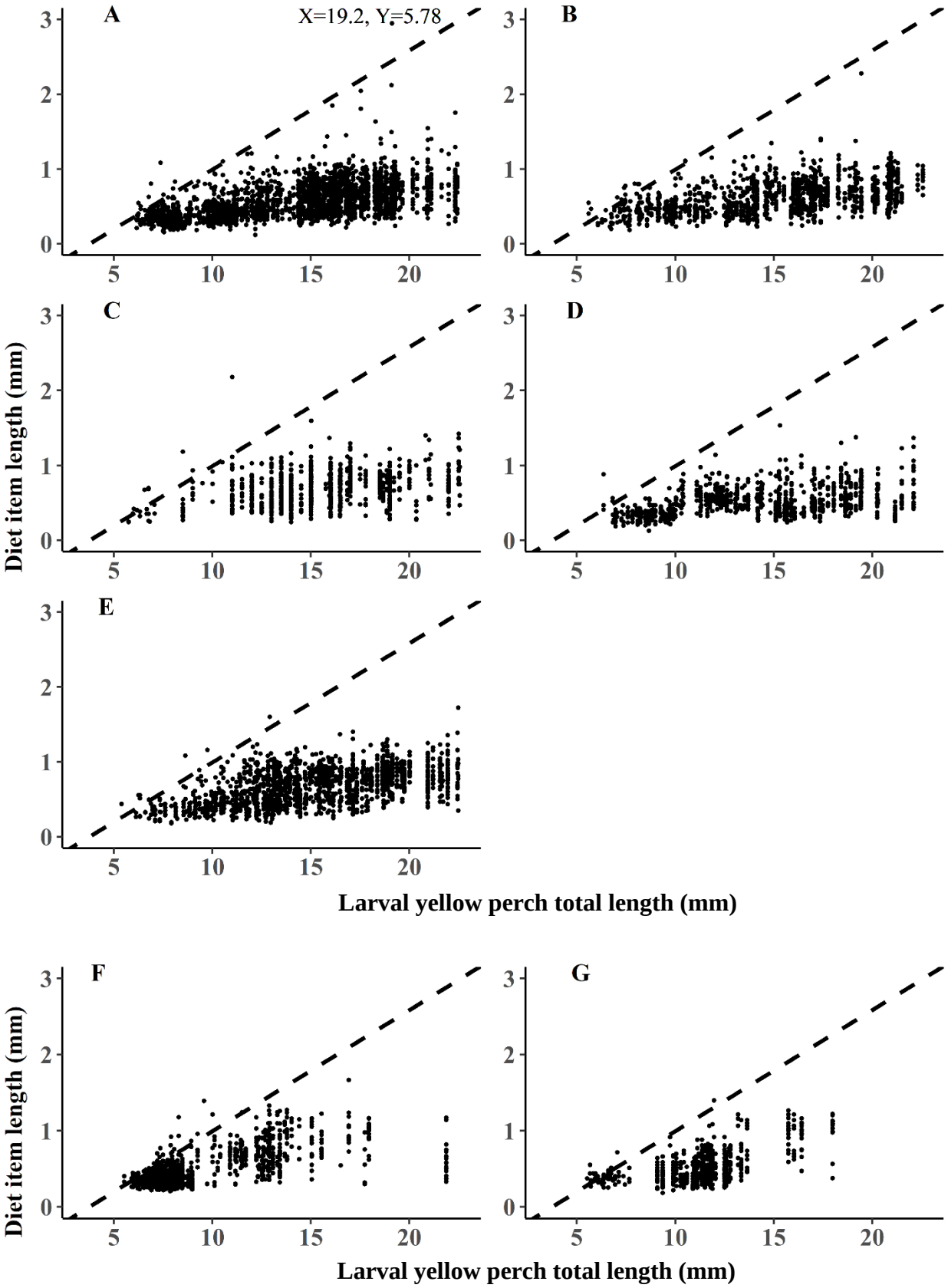

A
X=19.2, Y=5.78
B
C
D
E
F
G
Diet item length (mm)
Larval yellow perch total length (mm)
0
1
2
3
5
10
15
20

Figure 4

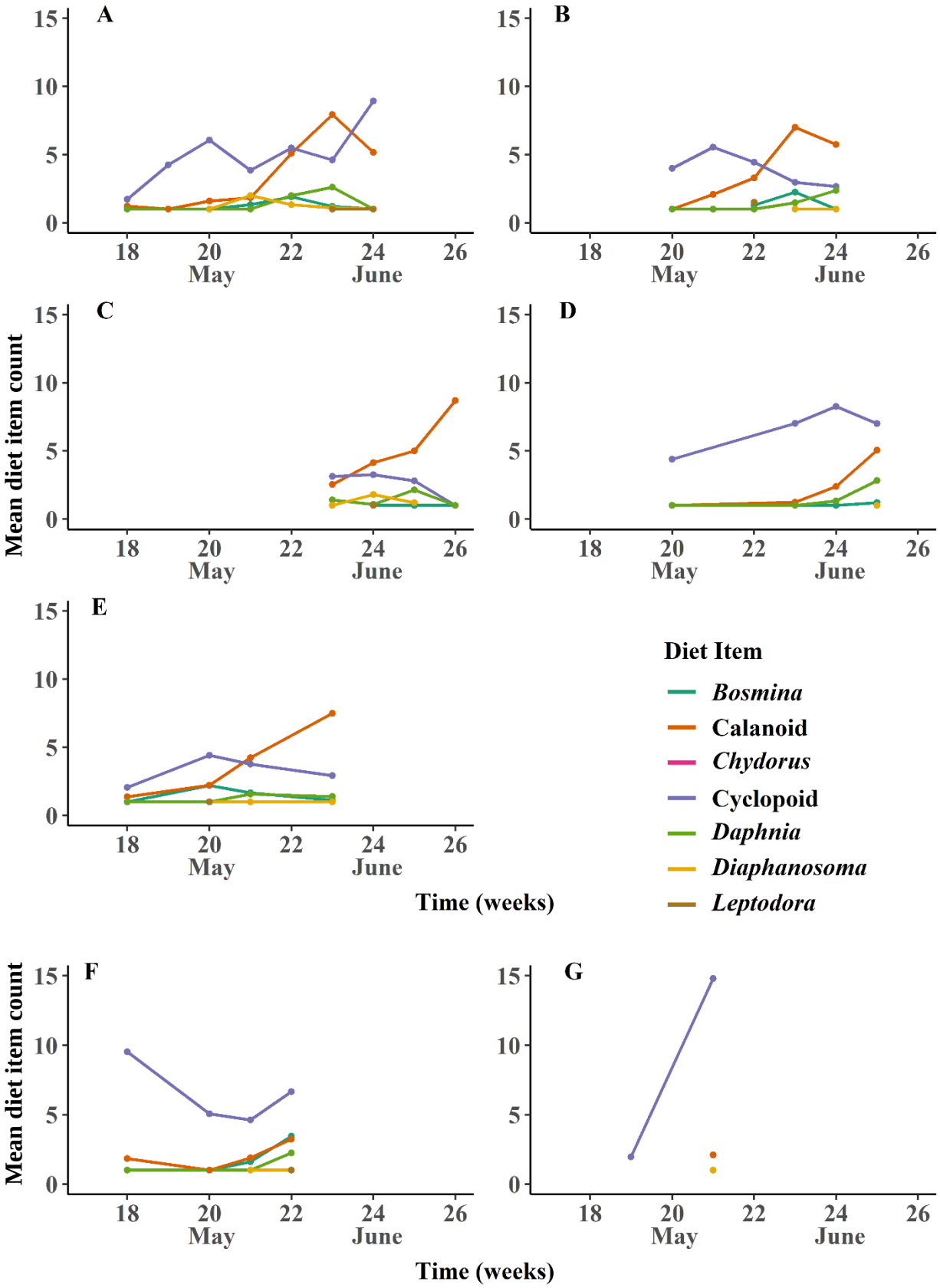

A
B
C
D
E
F
G
Mean diet item count
Time (weeks)
May
June
Diet Item
Bosmina
Calanoid
Chydorus
Cyclopoid
Daphnia
Diaphanosoma
Leptodora

Figure 5

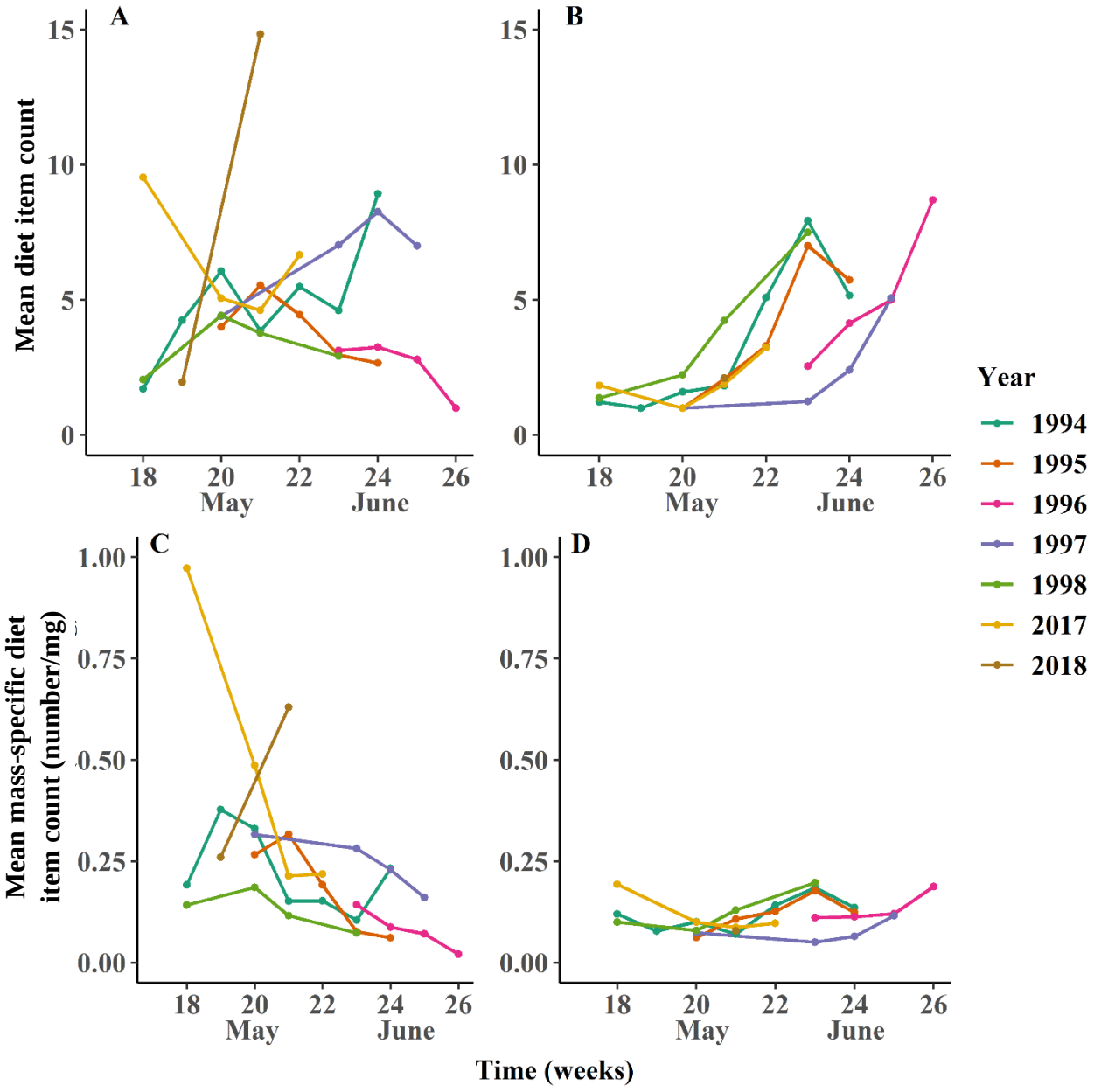

A
B
C
D
Mean diet item count
Mean mass-specific diet item count (number/mg)
Time (weeks)
15
10
5
0
1.00
0.75
0.50
0.25
0.00
18
20
22
24
26
May
June
Year
1994
1995
1996
1997
1998
2017
2018

Figure 6

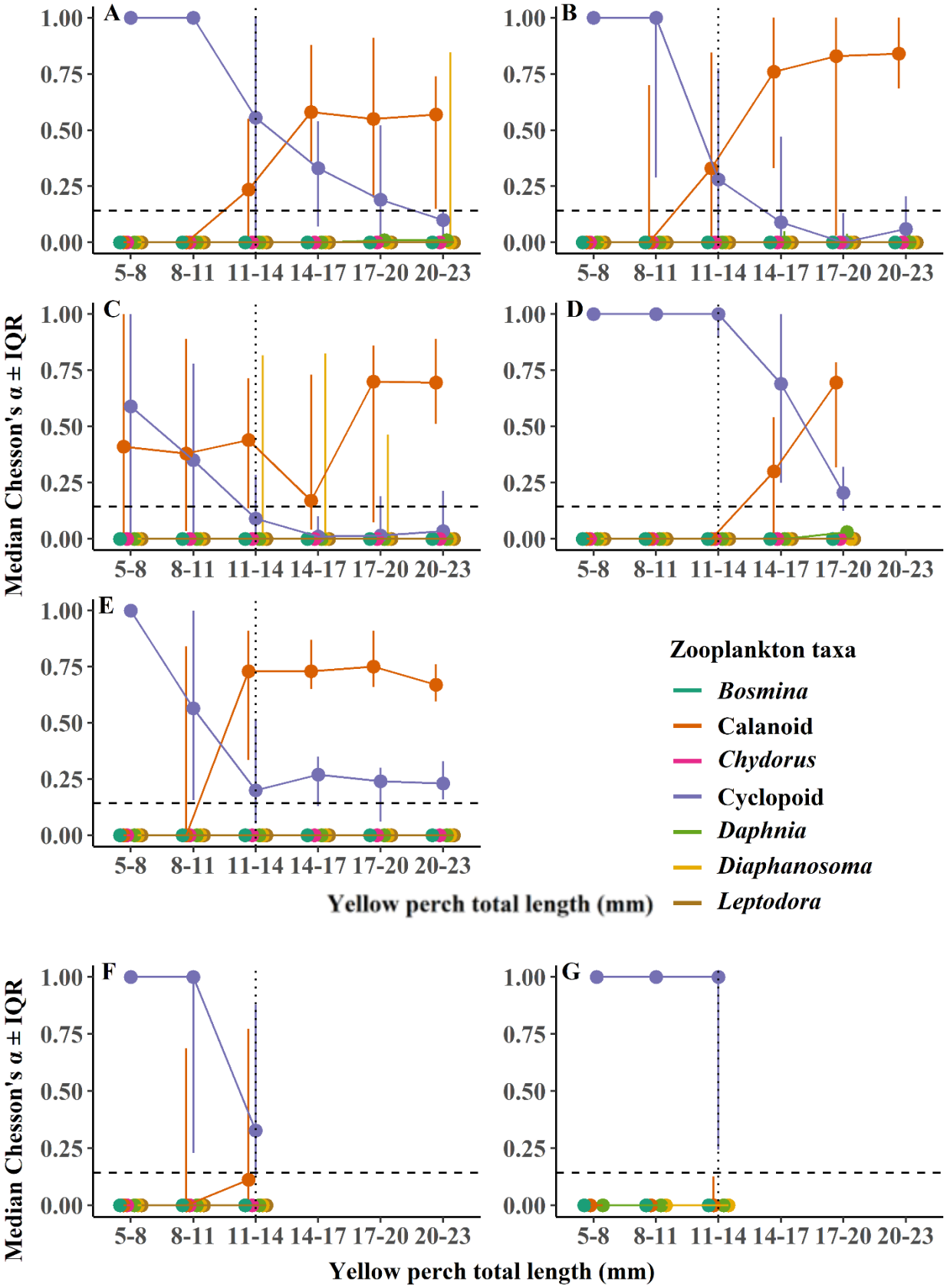

A
B
C
D
E
F
G
1.00
0.75
0.50
0.25
0.00
5-8
8-11
11-14
14-17
17-20
20-23
Median Chesson's α ± IQR
Yellow perch total length (mm)
Zooplankton taxa
Bosmina
Calanoid
Chydorus
Cyclopoid
Daphnia
Diaphanosoma
Leptodora

Figure 7

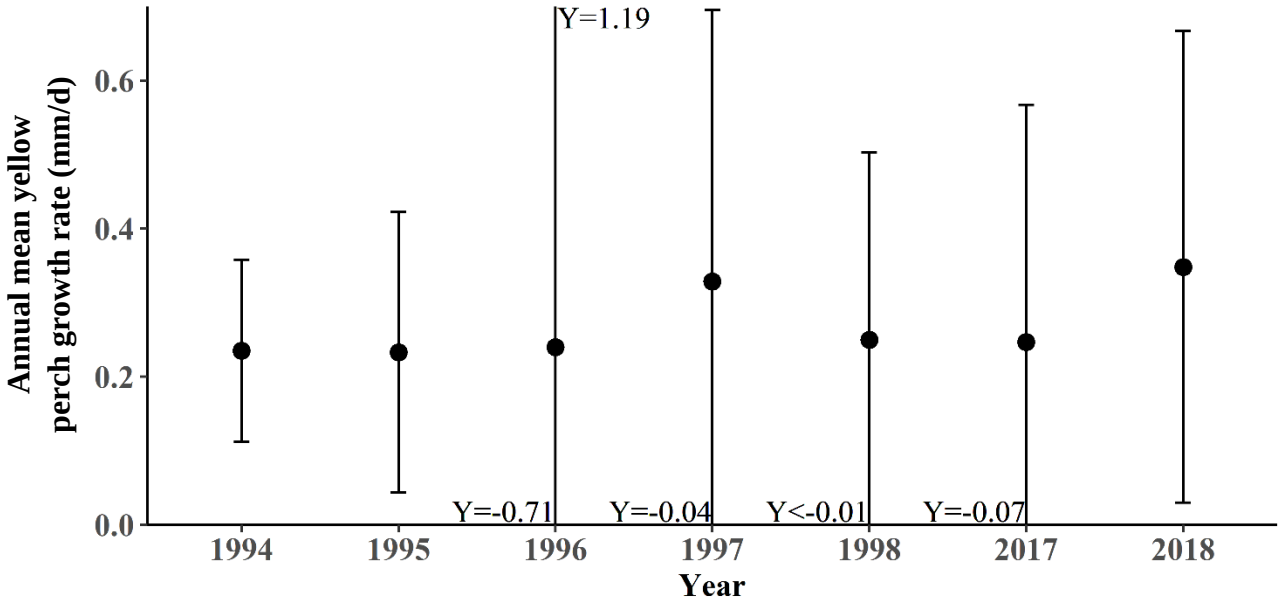

Annual mean yellow perch growth rate (mm/d)
0.0
0.2
0.4
0.6
Y=1.19
Y=-0.71
Y=-0.04
Y<-0.01
Y=-0.07
1994
1995
1996
1997
1998
2017
2018
Year

Figure 8

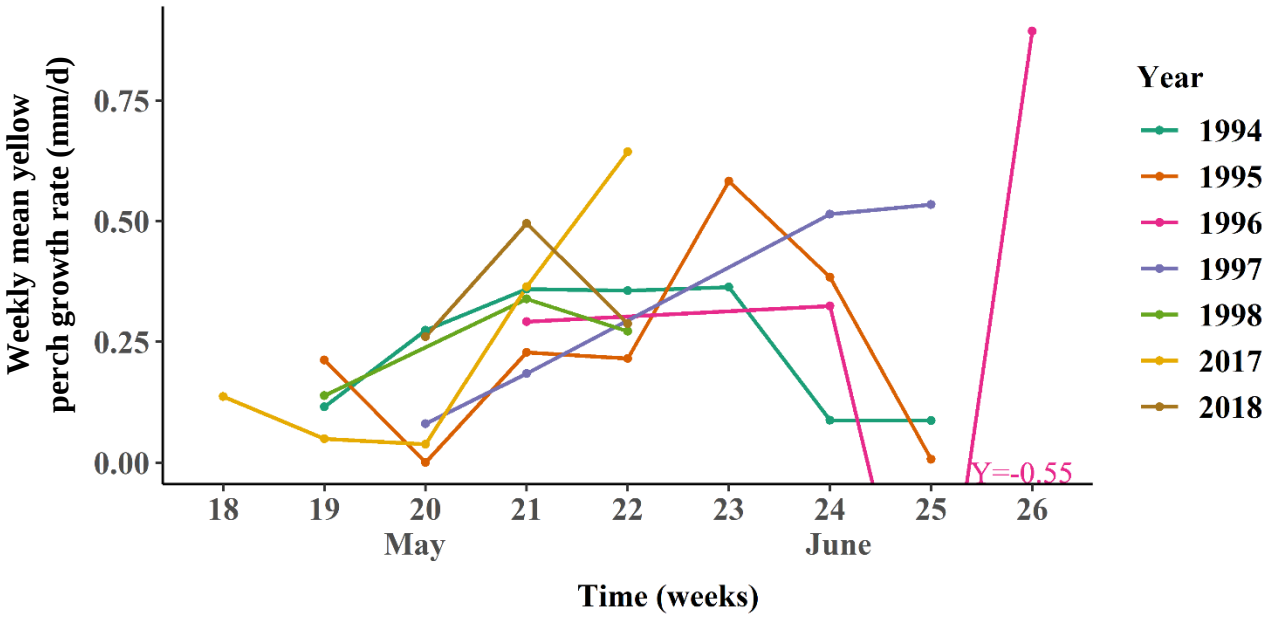

Weekly mean yellow perch growth rate (mm/d)
0.75
0.50
0.25
0.00
18
19
20
21
22
23
24
25
26
May
June
Time (weeks)
Y=-0.55
Year
1994
1995
1996
1997
1998
2017
2018

Figure 9

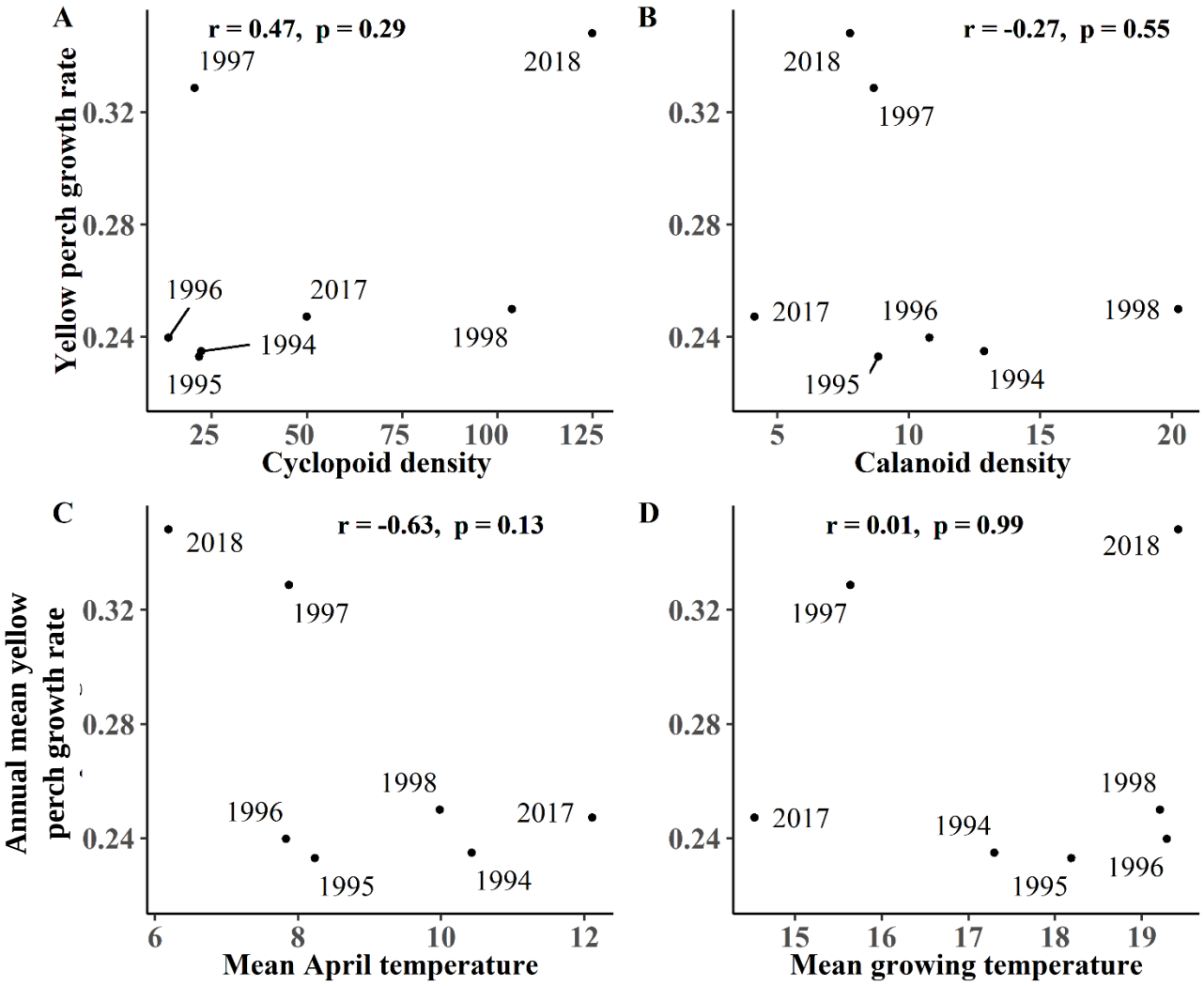

A
r = 0.47, p = 0.29
Yellow perch growth rate
0.32
0.28
0.24
1997
2018
1996
2017
1994
1998
1995
25
50
75
100
125
Cyclopoid density
B
r = -0.27, p = 0.55
2018
1997
2017
1996
1998
1995
1994
5
10
15
20
Calanoid density
C
r = -0.63, p = 0.13
Annual mean yellow perch growth rate
2018
1997
1998
1996
2017
1995
1994
6
8
10
12
Mean April temperature
D
r = 0.01, p = 0.99
2018
1997
1998
2017
1994
1996
1995
15
16
17
18
19
Mean growing temperature

Figure 10

Appendix A

Table A1. Pearson correlation coefficient (*r*) describing relationships between year, average growth rate (mm/d) of larval yellow perch, overall cyclopoid density (individuals/m^3), early cyclopoid density (individuals/m^3), overall calanoid density (individuals/m^3), late calanoid density (individuals/m^3), mean April temperature (ºC), and mean growing temperature (ºC) during 1994–1998, 2017, and 2018. All collections were made in Sandusky Bay, Lake Erie, during the spring. Early and late prey density refers to abundance of those prey items during weeks before and after the median length of yellow perch larvae collected reached the total length cutoff for diet preference change (12.8 mm; Supplemental Fig. A1), respectively, whereas overall prey density refers to the ambient abundance of those prey items averaged across all weeks in which larvae were collected.

	Year	Growth	Overall cyclopoid density	Early cyclopoid density	Overall calanoid density	Late calanoid density	Mean April temperature	Mean growing temperature
Year	1.00							
Growth	0.46	1.00						
Overall cyclopoid density	0.62	0.47	1.00					
Early cyclopoid density	0.49	0.31	0.97	1.00				
Overall calanoid density	-0.55	-0.27	0.25	0.42	1.00			
Late calanoid density	-0.43	-0.22	0.38	0.49	0.90	1.00		
Mean April temperature	0.04	-0.63	-0.19	-0.02	0.06	-0.10	1.00	
Mean growing temperature	-0.21	0.01	0.40	0.38	0.55	0.73	-0.59	1.00

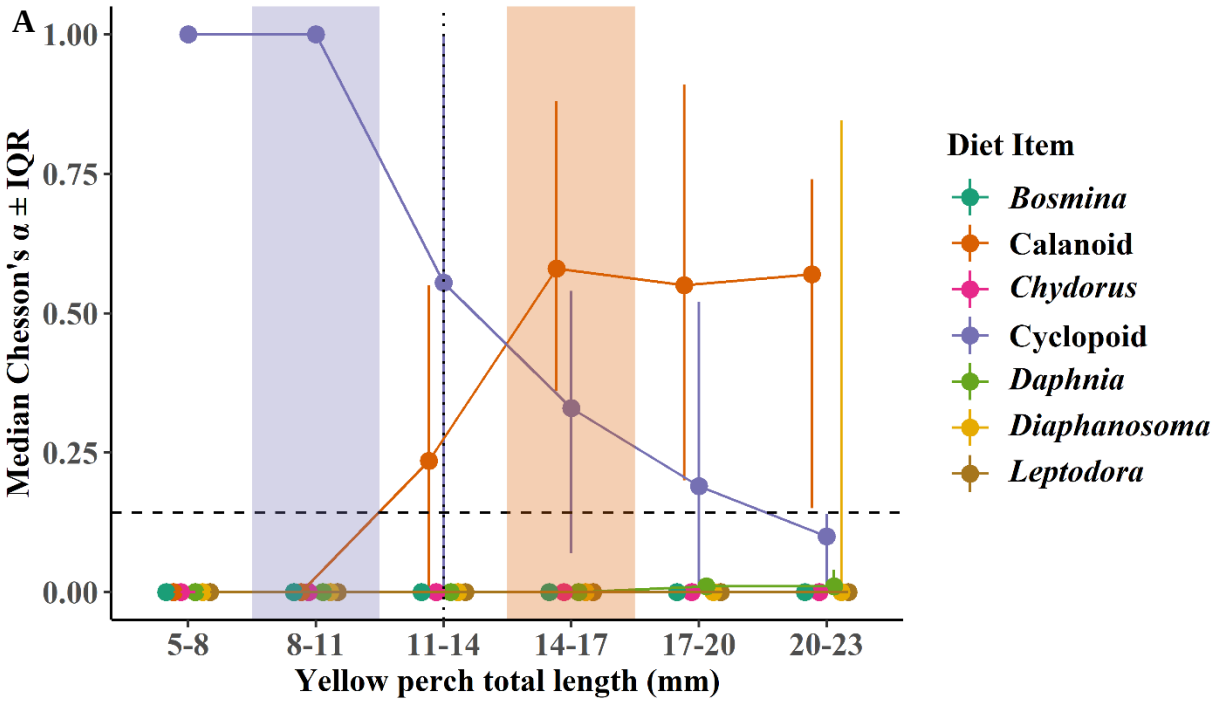
Table A2. Pearson correlation coefficient (*r*) describing relationships between year, average growth rate (mm/d) of larval yellow perch, overall cyclopoid biomass (μg/m^3), early cyclopoid biomass (μg/m^3), overall calanoid biomass (μg/m^3), late calanoid biomass (μg/m^3), mean April temperature (ºC), and mean growing temperature (ºC) during 1994–1998, 2017, and 2018. All collections were made in Sandusky Bay, Lake Erie, during the spring. Early and late prey biomass refers to abundance of those prey items during weeks before and after the median length of yellow perch larvae collected reached the total length cutoff for diet preference change (12.8 mm; Supplemental Fig. A1), respectively, whereas overall prey biomass refers to the ambient abundance of those prey items averaged across all weeks in which larvae were collected.

	Year	Growth	Overall cyclopoid biomass	Early cyclopoid biomass	Overall calanoid biomass	Late calanoid biomass	Mean April temperature	Mean growing temperature
Year	1.00							
Growth	0.46	1.00						
Overall cyclopoid biomass	0.89	0.56	1.00					
Early cyclopoid biomass	0.87	0.40	0.96	1.00				
Overall calanoid biomass	-0.21	-0.01	0.21	0.28	1.00			
Late calanoid biomass	0.16	0.27	0.58	0.51	0.78	1.00		
Mean April temperature	0.04	-0.63	-0.19	0.05	-0.12	-0.42	1.00	
Mean growing temperature	-0.21	0.01	0.18	0.09	0.71	0.77	-0.59	1.00

List of Figures

Figure *Page*

A



B

1. Year	2. Largest bin of selection for cyclopoids	3. Median larval YP length in largest bin of selection for cyclopoids	4. Smallest bin of selection for calanoids	5. Median larval YP length in smallest bin of selection for calanoids
1994	8–11	9.8	14–17	15.7
1995	8–11	9.5	14–17	15.9
1996	N/A	N/A	20–23	21.0
1997	14–17	15.3	17–20	18.5
1998	8–11	9.6	11–14	12.8
2017	8–11	8.8	N/A	N/A
2018	N/A	N/A	N/A	N/A

Figure A1

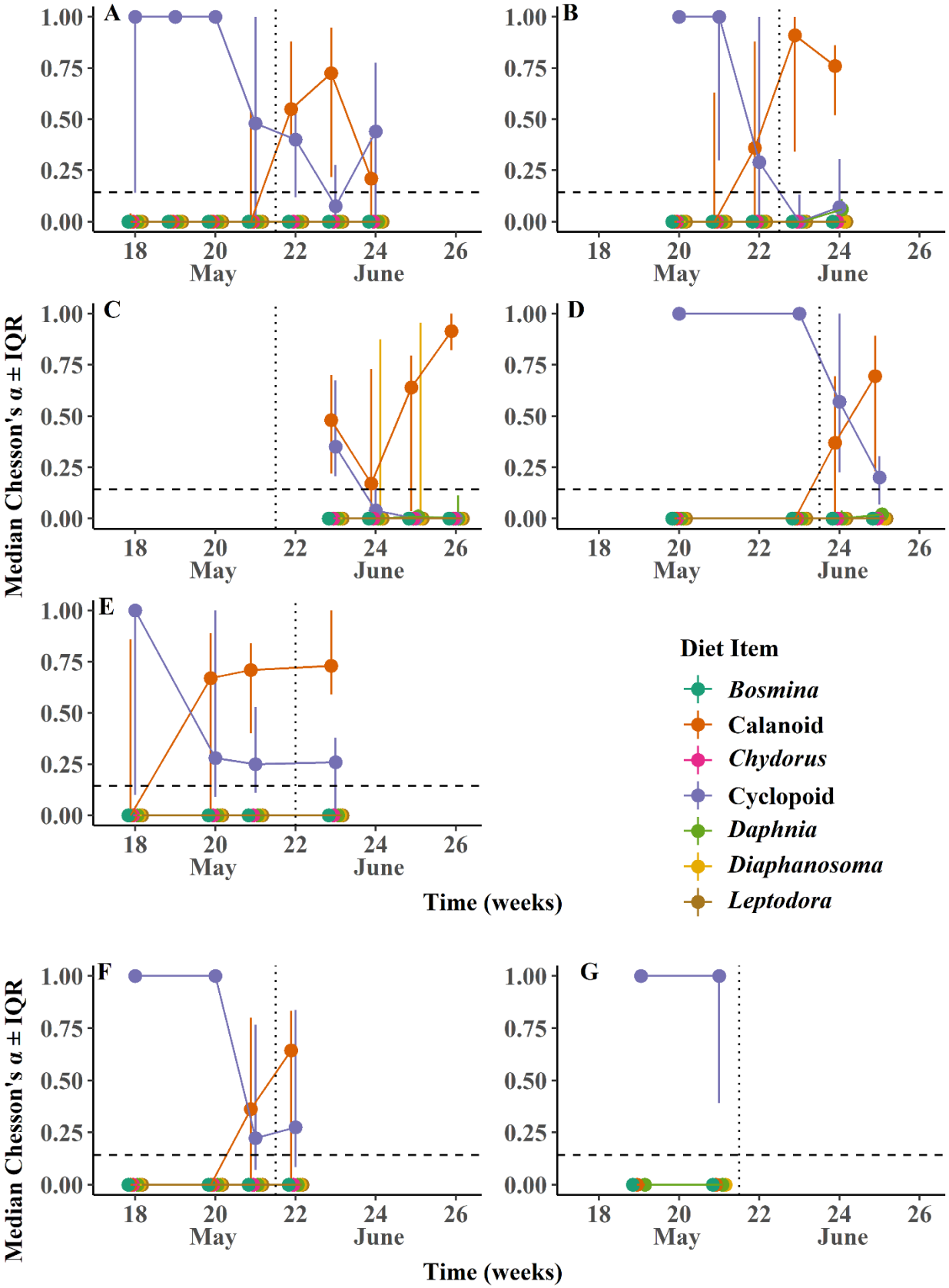

A
B
C
D
E
F
G
1.00
0.75
0.50
0.25
0.00
18
20
22
24
26
May
June
Median Chesson's α ± IQR
Time (weeks)
Diet Item
Bosmina
Calanoid
Chydorus
Cyclopoid
Daphnia
Diaphanosoma
Leptodora

Figure A2

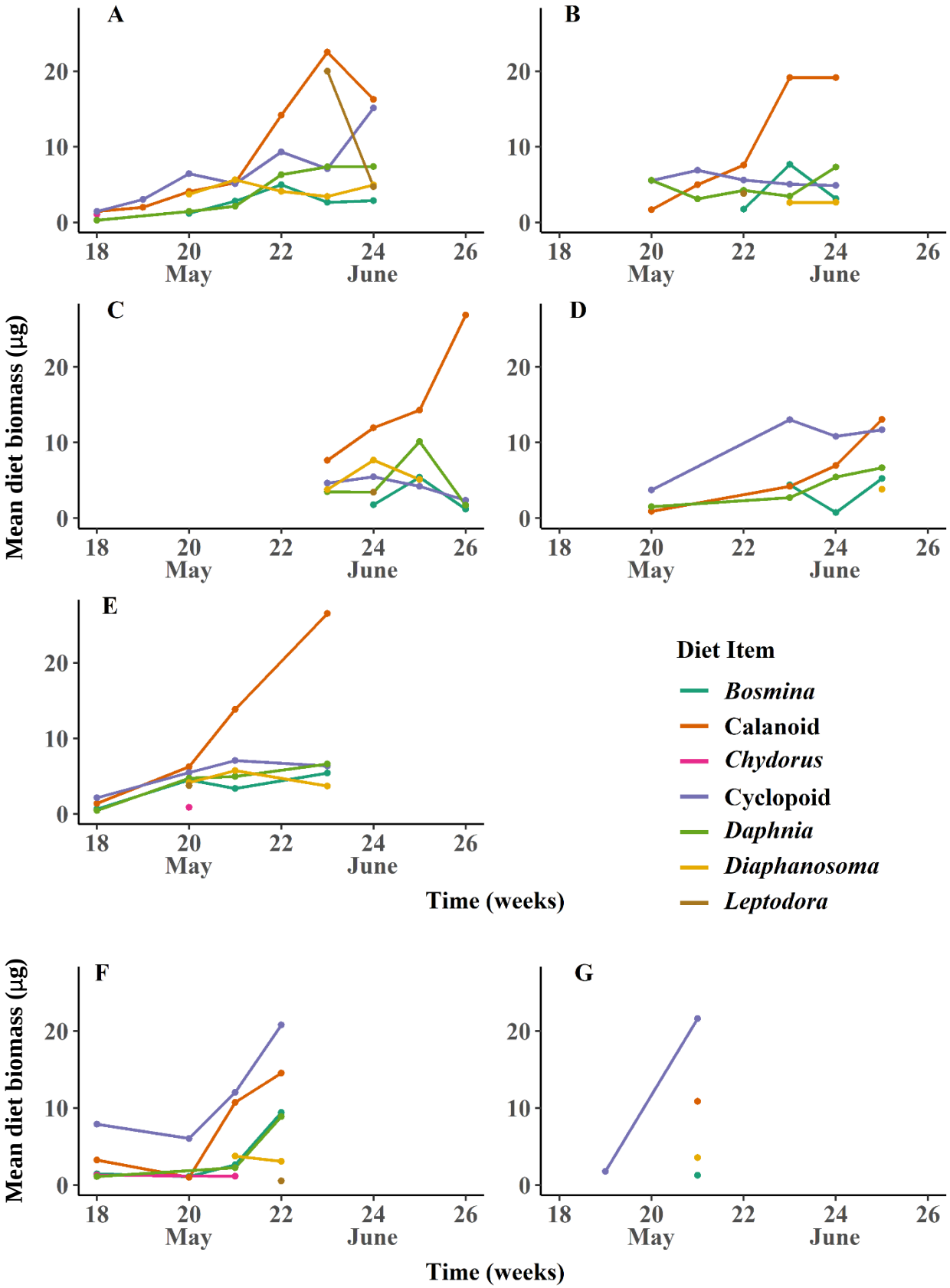

A
B
C
D
E
F
G
Mean diet biomass (µg)
Time (weeks)
0
10
20
18
20
22
24
26
May
June
Diet Item
Bosmina
Calanoid
Chydorus
Cyclopoid
Daphnia
Diaphanosoma
Leptodora

Figure A3

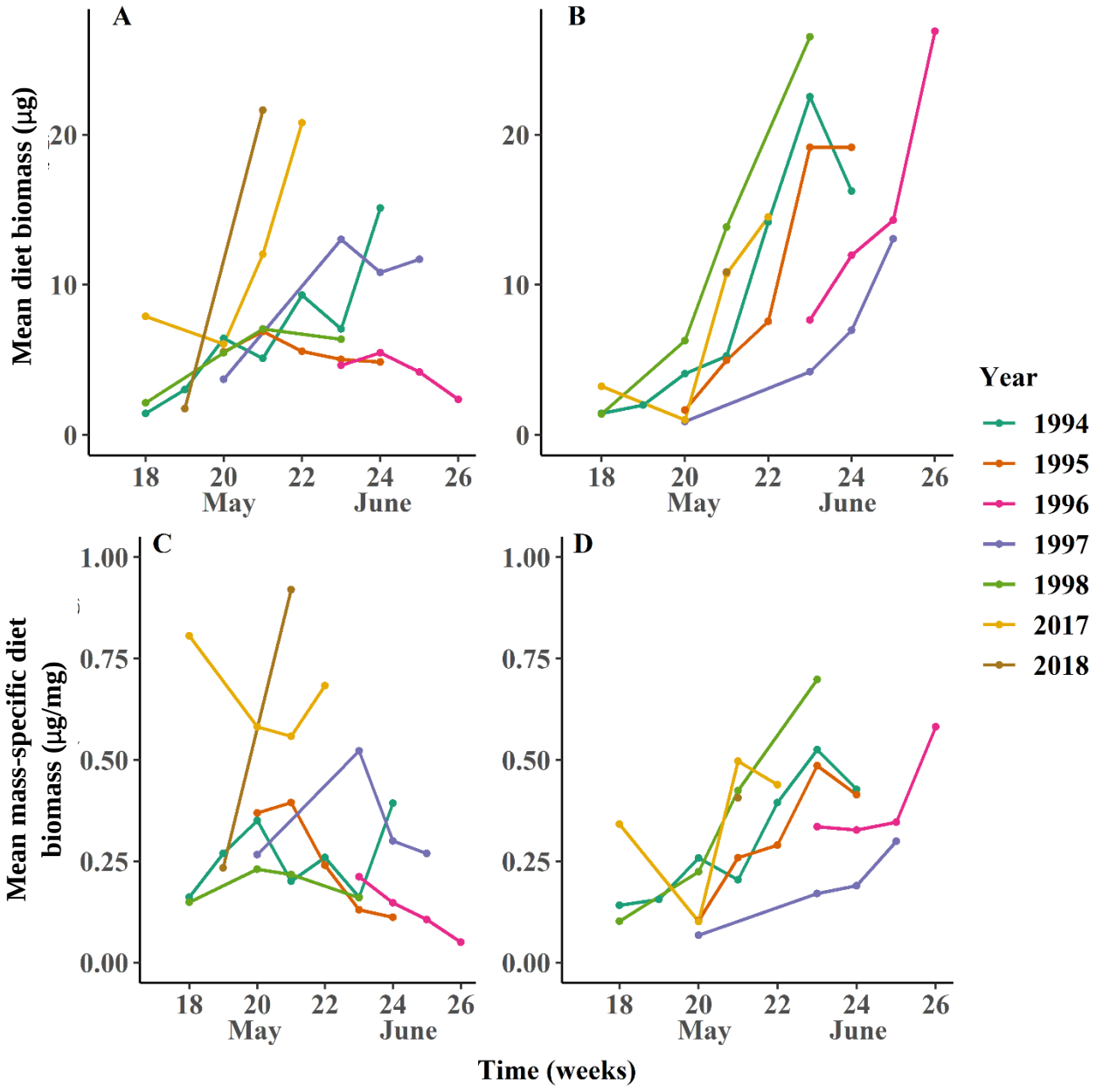

A
B
C
D
Mean diet biomass (µg)
Mean mass-specific diet biomass (µg/mg)
Time (weeks)
May
June
Year
1994
1995
1996
1997
1998
2017
2018

Figure A4